

CONSTRAINTS OF SEED SIZE ON PLANT DISTRIBUTION AND ABUNDANCE

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Abstract. We examined the correlation between seed size (mass) and spatial and temporal distribution and abundance of plants, using both published data from northern England and 18 years of census data from permanent quadrats in the Chihuahuan Desert, Arizona, USA. In both systems, there were many small-seeded species and few large-seeded ones. Spatial patterns of distribution and abundance were constrained by seed size within triangle envelopes, i.e., small-seeded species had a greater range of abundance and a greater number of sites occupied than did large-seeded species. Temporal patterns of abundance and distribution from the Chihuahuan Desert site were similarly correlated with seed size, i.e., small-seeded species were, in general, more abundant and present in more years than were large-seeded species. These patterns probably result because small-seeded species produce more seeds, are more vagile, and persist longer in seed banks than do large-seeded species. The results are consistent with recent findings from seed bank studies, suggesting the generality of the correlation between seed size and plant abundance and distribution.

Key words: Chihuahuan Desert, Arizona; constraint envelope; dispersal; England, northern; plant abundance; plant distribution; seed bank; seed size; triangular envelope.

INTRODUCTION

A positive relationship between distribution and abundance has been reported for many plant and animal species (reviewed in Gaston 1996), with a number of mechanisms proposed to explain such patterns (e.g., Hanski 1982, Brown 1984, Wright 1991). Recently, Hanski et al. (1993) postulated that dispersal ability should strongly influence the distribution of species, and suggested that when two species of identical abundance are compared, the species with the greater dispersal ability should be more widely distributed than the species of low dispersal ability (see Hanski et al. 1993: Fig. 10.1). To date, however, few studies of distribution and abundance have examined effects of dispersal (but see Rees 1995).

Seed size is a key and relatively stable life history trait that can be strongly related to dispersal ability and many other life history characteristics such as competitive ability (e.g., Thompson 1987, Michaels et al. 1988, Rees 1995), dispersal (e.g., Venable and Brown 1988, Westoby et al. 1990, 1992, Greene and Johnson 1993), dormancy (e.g., Venable and Brown 1988, Venable 1992), germination (e.g., Mazer 1989, Shipley and Parent 1991), growth rate (e.g., Shipley and Parent 1991), adult plant size (e.g., Leishman and Westoby 1994), flower size (Sakai and Sakai 1995), longevity of plants (e.g., Silvertown 1981), and seed bank per-

sistence (e.g., Thompson and Grime 1979; but see Leishman and Westoby 1998). Small-seeded species should have greater dispersal capacity, because small seeds are usually produced in greater quantity and are more readily transported by both abiotic and biotic dispersal agents (Venable and Brown 1988, Greene and Johnson 1993).

In a recent study of desert seed banks in the southwestern United States, however, Guo et al. (1998b, 1999) found that small seeds can have great ranges of abundance and distribution (i.e., can be either rare or abundant, and occupy few or many sites), whereas large seeds are always rare and occupy few sites. Thus, a "triangular" distribution of seed abundance or distribution is formed as a function of seed size. The structure and dynamics of seed banks are somewhat related to those of aboveground plant communities (Fenner 1985, Thompson 1987, Aguiar and Sala 1997). Therefore, whether the patterns found in seed banks also exist in aboveground plant communities, and whether seed size is correlated with plant abundance and distribution, are of particular interest.

In this study, we examine how seed size correlates with plant distribution and abundance by examining two sets of data. One consists of published census data from 10 sites in northern England (Thompson and Grime 1979); the other is a long-term census of annual plants from Portal, Arizona, in the Chihuahuan Desert. The Chihuahuan Desert site contains two communities of annual plants and allows an examination of the effects of seed size on spatial patterns of distribution and

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abundance (by examining data from a single year), as well as an examination of the effects of seed size on temporal distribution (the number of years a particular species was present) and temporal abundance (the mean abundance over years). We hypothesize that the above-ground plant community will show the similar "triangular" pattern observed in seed banks, i.e., small-seeded species can be abundant or rare and broadly or narrowly distributed, but larger-seeded species are always rare and distributed in fewer sites.

METHODS

Large-scale sites in northern England

Thompson and Grime (1979) collected data in 1974–1975 from 10 different sites that varied in vegetation composition within a 50×60 km area in northern England in order to compare community structure in established vegetation and associated seed banks (Fig. 1). These sites were covered by diverse vegetation types, including seminatural woodland, a hedge at a farmland, tall-herb grassland, waterlogged peat, and arable field; several sites were frequently disturbed by burning, grazing, or human activities. At each site, the frequency of occurrence of each species was recorded on 100 randomly distributed quadrats (each 10×10 cm). Details on the location of the 10 study sites, a brief description for each site, and seed identification procedure were given in Thompson and Grime (1979). We used data from their Appendix, which lists the abundance of each species at each site and corresponding seed mass data. The term "seed" in the original study included both seeds and fruits. Seed mass was calculated as the average mass in milligrams, based on collection of seeds from native populations in the Sheffield area. Because no actual number of individuals was provided in Thompson and Grime's (1979) original study, for the purpose of this study, plant abundance was estimated as the frequency of occurrence of each species across 100 randomly sampled quadrats at each of the 10 sites.

Small-scale Portal site

The field data were collected from a 20-ha long-term experimental study site established in 1977 near Portal, Arizona (Brown et al. 1986). Livestock have been excluded from the site since 1977. The vegetation is primarily upper-elevation Chihuahuan Desert scrub, consisting of scattered shrubs, half-shrubs, and grasses. The site receives a bimodal regime of annual precipitation and, correspondingly, supports two groups of annual plants (winter and summer annuals; Fig. 1).

The study site contained 24 experimental plots, each 0.25 ha in area, subjected to various experimental treatments. Within each plot were 16 permanent, regularly spaced quadrats, each 0.25 m² in area. All plants were counted individually by species in the 384 quadrats. Corresponding to the bimodal precipitation, we cen-

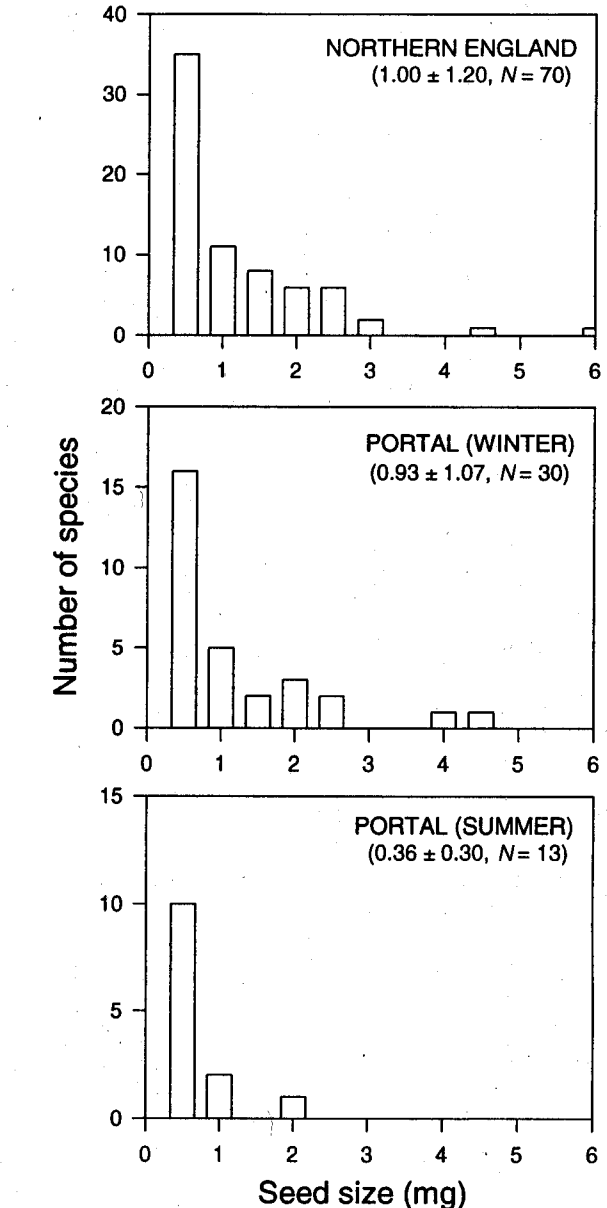


FIG. 1. Frequency distribution of seed sizes in three plant communities at the two study sites. Variation around the mean is expressed as ± 1 SE.

sused winter and summer annual plants, as well as bi-seasonal species and perennials twice each year, during April–May and August–September, beginning in 1978. Each census corresponded to the period of peak flowering and maximum biomass. To eliminate potential effects of the experimental treatments, all analyses were performed on data from the two original control plots (i.e., 32 quadrats). Spatial distribution was measured as the mean number of quadrats that a species occupied over 18 years. Temporal abundance was measured as the mean plant density across 32 1×1 -m² quadrats and over 18 years, and the temporal distribution was measured as the number of years that a species was present during the long-term study. Seed sizes were estimated by measuring seed mass. On av-

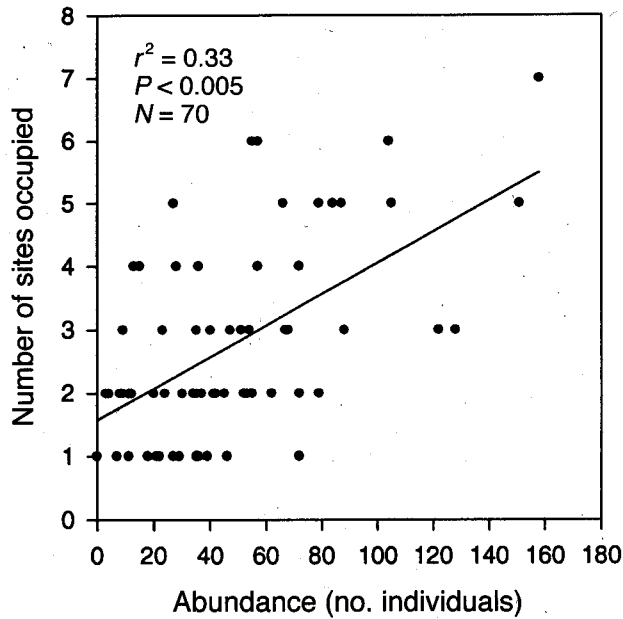


FIG. 2. Relationship between distribution (number of sites occupied) and abundance (number of individuals) measured at the northern England sites. Each symbol represents one species.

erage, winter annuals have larger seeds than do summer annuals (Brown et al. 1986, Guo et al. 1995).

RESULTS

Northern England sites

The original study revealed no close relationship between the relative proportions of species in the germinable seed reservoir and the species composition in the established vegetation at each site (Thompson and

Grime 1979). Our analyses determined that there was a significant positive relationship between distribution (the number of sites occupied by the species) and abundance (Fig. 2). Although regression analyses on both raw and log-transformed data did not exhibit any significant relationship between seed size and plant distribution (number of sites occupied) or abundance, these relationships can be well described by triangular envelopes (Fig. 3). In other words, small-seeded species had a greater range of abundance or number of sites occupied, but large-seeded species always had low abundance and were only found in a few sites.

Portal site

In both the winter and summer annual plant communities, seed size was negatively correlated with both temporal abundance and temporal distribution. Data were log-transformed prior to analyses because of the non-normality of the raw data (also for better fit); mean density vs. seed size: winter, $r = -0.51, P < 0.01$; summer, $r = -0.62, P < 0.005$; number of years present: winter, $r = -0.42, P < 0.005$; summer, $r = -0.73, P < 0.01$. Many of the relationships were distinctly triangular (Fig. 4). Large-seeded species tended to be present in only a few years during the study, and exhibited low levels of overall abundance. Small-seeded species exhibited either high or low overall abundance and were present in either many or few years.

Seed size was also significantly correlated with spatial distribution (measured by mean number of quadrats occupied over 18 years; winter: $r = -0.65, P < 0.01$; summer: $r = -0.76, P < 0.01$). Species with large seeds were restricted to a small proportion of quadrats, whereas species with small seeds occurred in either a

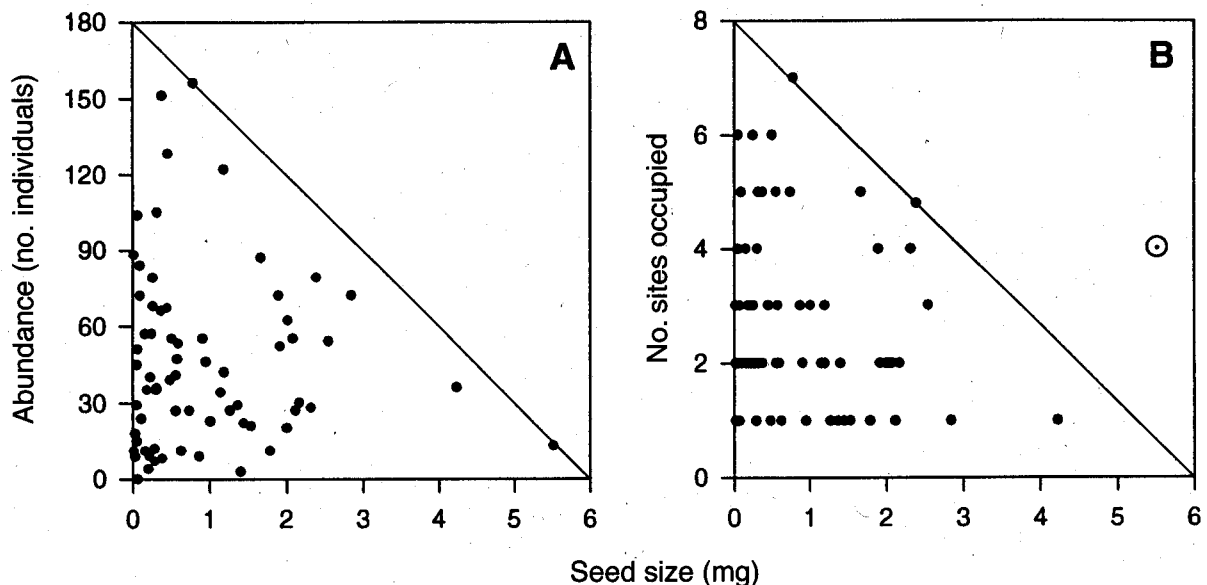


FIG. 3. Relationships (A) between abundance and seed size and (B) between distribution (number of sites occupied) and seed size at the northern England sites. Each symbol represents a species; the circled dot represents an outlier that was included in randomization tests.

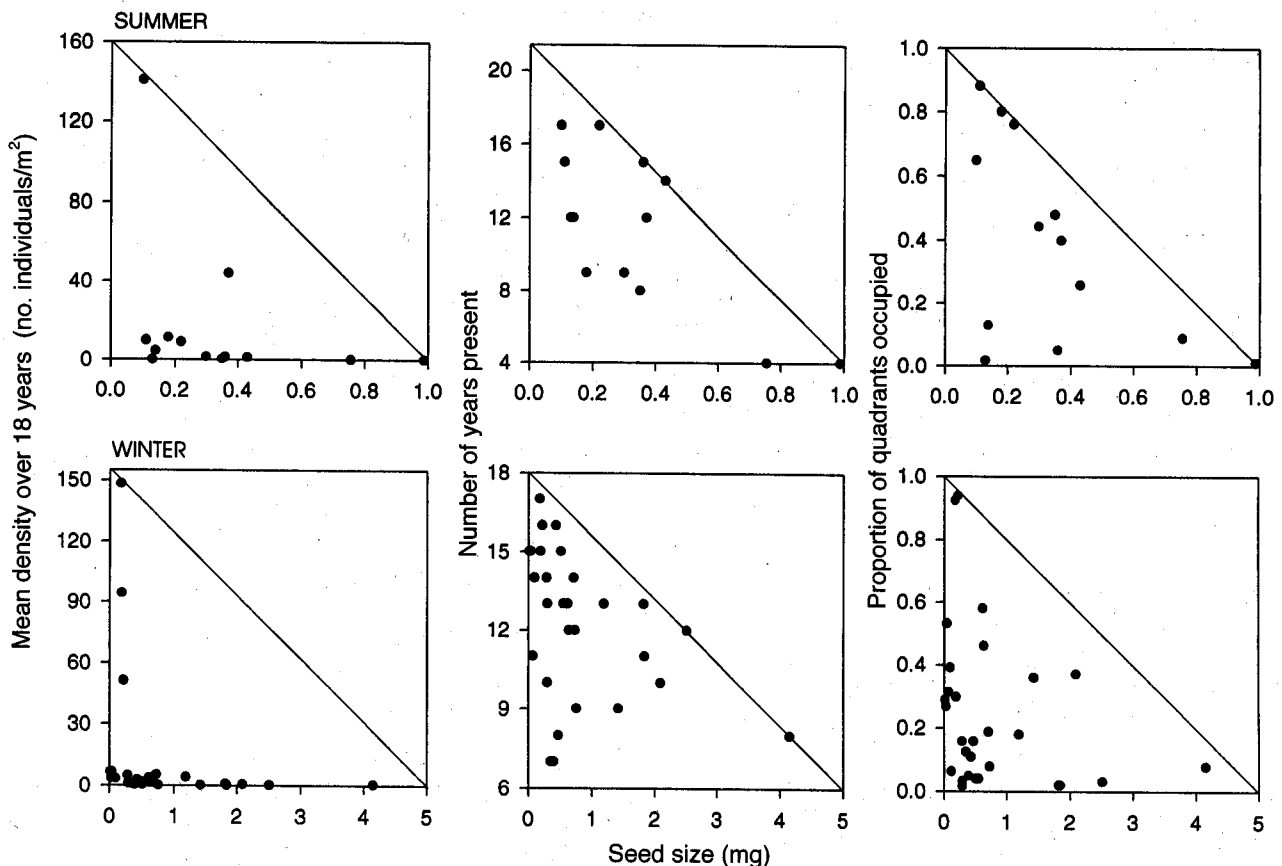


FIG. 4. The relationship between mean plant density (left), number of years present (middle), or distribution (right) and seed size for both summer (above) and winter (below) annual communities at the Portal site, Arizona. Note that the x-axis scales are different for summer and winter annuals; because of the much smaller seeds of summer annuals. Each symbol represents a species.

large or small proportion of quadrats ("envelope" effects; Fig. 4). Small-seeded species were widely distributed over space, whereas large-seeded species were highly restricted in spatial distribution (Fig. 4). The spatial distribution, mean abundance over 18 years, and the number of years in which the species were present were significantly correlated. Details on these relationships will be reported elsewhere (Guo et al. 2000).

Statistical (randomization) tests

To examine whether any relationships between plant abundance (or distribution) and seed size can be distinguished from null hypotheses of random association, we performed randomization tests. These tests were also used to evaluate the extent to which the data points for each species group fell within a hypothesized "triangular envelope" of the abundance (or distribution)–seed size relationship. The hypothesized triangular envelope was constructed by connecting the data point with the highest abundance with a second data point, such that the resulting triangular envelope contained all of the remaining data points. We then tested the null hypothesis by comparing the area of the triangular envelope with the areas of triangular envelopes generated by random combinations of abundance (or distribution)

and seed size. The values of abundance or distribution (number of sites) of a species were paired with a seed size drawn at random from the raw data. We repeated this process, drawing values for each species without replacement until all values were drawn. This procedure produced a randomized species assemblage containing the same number of species and the same distribution of values as the real communities. For each such random species assemblage, the area of a hypothetical triangular envelope was computed; this procedure was repeated 5000 times. The probability of obtaining this result under the null hypothesis was estimated by determining the number of simulated values that were less than or equal to the observed value. This procedure was performed for both abundance and distribution (number of sites occupied) for the Northern England sites and the Portal site (including temporal distribution or the number of years present). Such randomization tests were performed separately for each plant community, including the winter and summer annual assemblages at Portal (for a similar randomization test, see Enquist et al. 1995).

Randomization tests of the observed data showed that, at the England sites, the null hypothesis of no association between abundance and seed size was re-

TABLE 1. The observed area of the triangular envelope and the *P* values for testing the null hypothesis of no association between abundance (or distribution) and seed size for each community.

Parameter	Portal, Arizona, USA					
	Northern England		Winter		Summer	
	Area	<i>P</i>	Area	<i>P</i>	Area	<i>P</i>
Abundance	541	0.046	322	0.152	77	0.007
log(Abundance)	38	0.073	9	0.047	3	0.168
Spatial distribution (no. sites)	44	0.192	2	0.039	1	0.001
Temporal distribution (no. years)	70	0.010	14	0.008

jected ($P < 0.05$), but our test failed to detect any significant relationship between distribution (number of sites occupied) and seed size (Table 1). Randomization tests of the observed data at the Portal site also showed that the null hypothesis of no significant association between seed size and spatiotemporal abundance or distribution was rejected for both winter and summer annuals (the lone exception was winter annuals, using raw abundance data; see Table 1).

DISCUSSION

Our results demonstrate that seed size is correlated with plant distribution and abundance, both in space and over time, and these relationships can be described by triangular "envelopes" (Figs. 3 and 4). Spatially, small-seeded species exhibited a wide range of abundance and distribution, whereas larger-seeded species always exhibited lower abundance and narrower distribution. The overall negative relationships between seed size and abundance or distribution are consistent with findings from eight British sand dune systems, where annual plant abundance and distribution were also negatively related to seed size (Rees 1995). Over time, small-seeded species tended to be present in more years than did large-seeded species. Despite the lack of close correspondence between the species composition of the seed flora and that of the associated vegetation (Thompson and Grime 1979, Aguiar and Sala 1997), the correlation between seed size and plant abundance and distribution were very similar to the recent reports on seed banks in desert ecosystems (e.g., Guo et al. 1998b, 1999), indicating the influence of seed size on both seed and plant abundance and distribution in these ecosystems.

We suggest that seed size affects distribution-abundance patterns in at least five ways. First, seed size affects abundance because there is a trade-off between seed size and number: small-seeded species produce more propagules than do large-seeded species (Harper et al. 1970, Greene and Johnson 1993). Second, seed size affects distribution, because small seeds are more readily dispersed than large seeds, especially in deserts where wind and water are the primary dispersal agents (Nelson and Chew 1977). Third, small seeds in soil seed banks can live longer than larger seeds (e.g., Harper et al. 1970). This increases the chances that small-seed-

ed species will germinate before predation and decay (Silvertown 1981). Fourth, large seeds suffer greater and highly selective predation by small mammals and birds, which tends to suppress the abundance of large-seeded annuals relative to small-seeded ones (Guo et al. 1995). Finally, there may be an evolutionary component; species with narrow environmental requirements may tend to evolve larger seeds that tend to disperse shorter distances, keeping offspring in micro-environments similar to those of their parents (Templeton and Levin 1979). Thus, there are many, non-mutually exclusive, reasons to expect that species with small seeds would have higher abundance and broader distribution.

For plants, vagility or dispersal ability is negatively correlated with seed size (mass) (Rees 1995). Our data suggest that dispersal ability, as inferred from seed size, simultaneously affects both the abundance and distribution of annual plants. Species with greater dispersal ability had wider distribution and greater abundance than did species with low dispersal ability. Although it has been suggested that seed shape and other characteristics of seeds can affect seed dispersability, such effects appeared to be limited, as the size-related variation falls within well-defined constraint envelopes of seed size. Large-seeded species with wings, hooks, or other appendages on the seeds that might promote seed dispersal still have lower abundance and narrower distributions, probably due, in large part, to smaller number of seeds.

Identifying the upper constraint lines of the triangles is critical for examining number-size trade-offs or the maximum abundance and distribution of a species with a certain average seed size. We may not have been able to predict the exact abundance or distribution of a species based on seed size, but we may be able to predict the maximum limitations on the abundance or distribution of a species with a known seed size (Brown and Maurer 1987, Brown 1995, Guo et al. 1998a, 1999). In our case, dispersal ability that is determined by seed size (mass) and number could be the limiting factor that controls the upper boundaries of the constraint envelope. Displacement of data points below the upper boundary may be due to diseases, life history (e.g., dispersal syndrome), and many other unknown factors. For example, a newly formed species, even one having

many small seeds, may still have a restricted spatial distribution. It simply may not have had sufficient time to spread over a large geographical area (Willis 1922).

Seed number–size trade-offs may occur both among individuals within a species (e.g., Smith and Fretwell 1974, Venable 1992) and among species within communities. Within angiosperms, seed size varies over 10 orders of magnitude among species (Harper et al. 1970, Michaels et al. 1988, Leishman and Westoby 1994), and this may partially explain the great variation in different species of plants on earth. Interestingly, in the Chihuahuan Desert, although summer annuals have much smaller seeds than winter annuals, both communities showed similar relationships (triangular envelopes) between seed size and distribution or abundance (Fig. 4), suggesting that such constraint envelopes may be more strongly expressed within, rather than across, communities. The relative abundance and distribution of component species in any particular community are ultimately controlled by constraints on covariation in these (and other) variables (Preston 1962, May 1975, Brown 1984, Brown et al. 1995, Rees and Westoby 1997).

A possible statistical bias may provide an alternative explanation for the observed triangular patterns: in any community there tend to be many small-seeded species and few large-seeded ones (W. Shipley, *personal communication*). However, such statistical bias cannot explain the exact triangular forms of the observed relationships, in which the large-seeded species will always be positioned in the lower right corner of the triangle. In other words, a simple statistical relationship or the null hypothesis of random association among the traits cannot explain why large-seeded species are always low in abundance and restricted in distribution. We tested this alternative hypothesis by conducting a series of randomization tests, which demonstrated that the patterns we observed are not simply the result of a statistical artifact. Further evidence to reject the statistical artifact hypothesis comes from the ubiquity of triangular relationships between size and measures of distribution and abundance. The effects of seed size on abundance and distribution of seeds in the soil seed banks also are observed for vegetative plants.

We believe that the patterns observed in our study may represent a general rule for the assembly of plant communities. We have outlined five mechanistic explanations for the observed relationships among distribution, abundance, and seed size, but these may not apply to all ecosystems. For instance, the persistence times of seeds in the soil may not always be affected by seed size as postulated (see Leishman and Westoby 1998). In addition, the systems that we examined contained seed sizes of limited range (<1.0 mg). Additional empirical investigations are required to determine whether communities containing even larger seeded species exhibit similar patterns.

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